

DOMINANCE-SPECIFIC VIGILANCE IN THE TUFTED TITMOUSE:
EFFECTS OF SOCIAL CONTEXT¹

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The hypothetical benefits accruing to animals participating in foraging groups are of two classes, improved predator avoidance and enhanced foraging efficiency (reviewed by Krebs and Davies 1987). These two classes of benefits often are not independent; for example, there is a growing literature demonstrating that the size of the foraging group influences how individuals' time budgets are apportioned among such antagonistic activities as vigilance for predators and foraging (e.g., Pulliam 1973, Powell 1974, Caraco 1979, Barnard 1980, Bertram 1980, Caraco et al. 1980a, Elgar and Catterall 1981, Lendrem 1983, Studd et al. 1983, Elgar et al. 1984). Several studies on how birds make this trade-off between foraging efficiently and avoiding predators have demonstrated that as flock size increases the proportion of time allocated by individuals to foraging activities is increased, while the flock's aggregate vigilance level is maintained or even increased (e.g., Powell 1974, Siegfried and Underhill 1975, Caraco 1979, Jennings and Evans 1980, Sullivan 1984a).

Most previous studies have failed to consider that individuals differing in dominance status probably experience different benefits and costs associated with flock membership (but see Moore 1972, cited in Caraco 1979; Caraco 1979; Ekman and Askenmo 1984; Ekman 1987). In particular, the time available for foraging should be more constrained for subordinates if higher-ranking conspecifics interfere with their foraging. The present study addresses experimentally the possibility that subordinates are more vigilant than dominants because they must keep higher-ranking conspecifics under surveillance to avoid aggressive interactions while also remaining vigilant for predators (cf. Robinson 1981, Waite 1986). Using captive Tufted Titmice (*Parus bicolor*), I examined the nonexclusive hypotheses that socially foraging animals are vigilant for (1) predators and (2) other foraging group members and, thus, vigilance is subject to control by at least two proximate factors, group size and dominance status, respectively. One prediction can be generated from each of these hypotheses, respectively: (1) a dominant titmouse should be more vigilant when foraging solitarily than when foraging as a member of a dyad, and (2) a subordinate titmouse should be more vigilant than a dominant titmouse when they forage together.

METHODS

Four pairs of wild-caught Tufted Titmice were housed in a large indoor aviary 4.8 m × 4.2 m × 2.7 m high between 19 December 1984 and 5 March 1985. To permit instant recognition of individuals, each bird's cheek patches were painted a unique color with waterproof felt tip markers. As Tufted Titmice are sexually monomorphic and difficult to sex reliably on the basis of external features, and as the birds in this study were neither sacrificed nor laparotomized, the sex of the birds was inferred on the basis of wing cord length, body mass, and whether singing occurred. The dominant individual in three replicates was a putative male, and in the fourth replicate a putative female. The subordinate individual in two replicates was a putative female. The sex of the subordinate bird in the other two replicates could not be determined using the above criteria. To ensure that the titmice had been familiar with each other in the wild, the birds of each dyad were captured contemporaneously at a single trapping station. The birds were held at $18.6 \pm 1.5^\circ\text{C}$ ($\bar{x} \pm \text{SE}$) on natural photoperiod, and were maintained on an ad libitum diet of sunflower seeds (*Helianthus* sp.) and mealworms (*Tenebrio* sp.). In order to be able to calculate rates of feeding in kcal hr⁻¹, the energetic contents of sunflower seeds (0.227 kcal seed⁻¹) and mealworms (0.086 kcal mealworm⁻¹) were determined (Lancaster Labs., Lancaster, Pennsylvania; details in Waite 1986). Each dyad of titmice had been used in other experiments (Waite 1986), and had been part of a captive mixed-species flock that was comprised of a male and a female Downy Woodpecker (*Picoides pubescens*), a male and a female White-breasted Nuthatch (*Sitta carolinensis*), two Carolina Chickadees (*Parus carolinensis*), and a third Tufted Titmouse. Each titmouse had been exposed to four playbacks of a Tufted Titmouse alarm call on a single day within the 4-day period prior to this study (Waite 1986). In addition, while held as a member of a captive mixed-species flock, each titmouse had been exposed to an overflight of a one-half life-size model of a Sharp-shinned Hawk (*Accipiter striatus*, unpubl. results). Thus, it is assumed that the titmice perceived some risk of predation during this study. Details concerning the aviary and the conditions under which the birds were held are in Waite (1986).

After the three Tufted Titmice had spent at least 3 days acclimating to the aviary as members of a mixed-species flock, dominance relationships among them were determined. This was accomplished by recording, during 20 15-min observation sessions, all interactions

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in which one bird used a supplanting attack or aerial chase against another titmouse.

The general experimental procedure was as follows. On at least the 10th day of captivity for each mixed-species flock, the Downy Woodpeckers, White-breasted Nuthatches, Carolina Chickadees, and the Tufted Titmice intermediate in dominance status were removed from the aviary, leaving only the dominant and subordinate titmice. I then observed the titmice each of the next 3 days beginning between 09:45 and 11:25 in one of the following contexts: subordinate solitary, dominant solitary, and foraging socially (subordinate with dominant present and dominant with subordinate present). For each dyad of titmice, the order of these three contexts was generated from a random-numbers table. Observations of birds of each dominance status foraging socially were made on the same day (order determined by a coin toss). Irrespective of dominance status and social context, trials lasted 72.8 min (SD = 17.6 min) on average. All supplanting attacks and chases occurring during these trials were recorded. During the observations of solitary individuals, the birds were in both visual and acoustic isolation from one another.

In each trial, the focal bird was observed as it arrived at a 0.6 m × 0.6 m feeding tray positioned 1.5 m above the aviary floor. The time lag between the beginning of a trial and the focal bird's first visit to the feeder averaged 6.6 min (SD = 5.0) and was statistically unrelated to either dominance status or social context (paired *t*-tests, all Bonferroni's *P*s > 0.77; Snedecor and Cochran 1967). No food was consumed during this interim; however, the titmice presumably were relatively well-fed at the onset of all trials as they had been housed in the test arena and allowed continuous free access to the feeder since dawn. As an index of vigilance, I recorded the time spent scanning at the feeder (Lendrem 1983). After arriving at the feeding table, birds often would remain immobile for 1 to 5 sec, and sometimes for as long as 16 sec. During this brief "freeze," they habitually assumed a very erect posture while moving the head from side to side, apparently scanning the environment. For each of 15 consecutive visits to the feeder by the focal bird that resulted in the consumption of a food item (always fewer than 19 and 23 total visits by dominants and subordinates, respectively), I recorded the elapsed time, to the nearest second, between alighting on the feeder and either the first perch change or the first lowering of the head such that the axis of the bill dropped below the horizontal. Either of these behaviors was followed almost invariably by the grasping of a food item with the bill. Any subsequent scanning during a single visit to the feeder was not recorded. Scanning at the feeder could be measured unambiguously, and appears a reasonable index of the extent to which individuals are sensitive to the risk of imminent attack by a predator (Lendrem 1983) or supplanting attack by a conspecific. In only one of the 16 observation sessions was there a significant correlation between time spent scanning at the feeder and the order of visits (solitary subordinate in replicate 4; $r = -0.608$, $P = 0.016$, two-tailed). In addition, a visual inspection of scanning durations over the three days of trials ($\bar{x} \pm \text{SE}$: 2.1 ± 0.6 sec, 1.5 ± 0.6 sec, and 2.9 ± 1.2 sec, respectively), independent of dominance status and social context, did not reveal

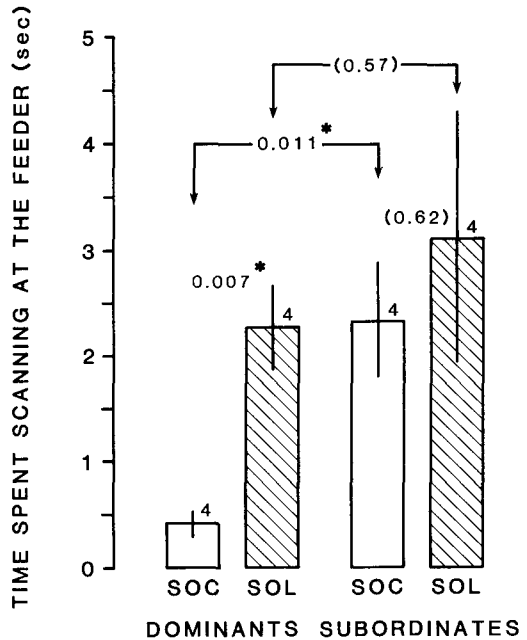


FIGURE 1. Time spent scanning at the feeder by dominant and subordinate Tufted Titmice in two contexts, social (i.e., as a member of a dyad) and solitary. The bars represent the mean of means for four replicates, and vertical lines indicate ± 1 SE. *P*-values are for paired *t*-tests. Parentheses indicate two-tailed tests; others are one-tailed. Asterisks indicate statistical significance after applying Bonferroni's probabilities technique for multiple comparisons to achieve a 0.05 experimentwise error rate (Snedecor and Cochran 1967).

any clear-cut pattern. Thus, the assumption that the perceived risk of attack by a predator or dominant conspecific was constant throughout the experiment appears justified.

Multiple comparisons among results from the two social contexts and two dominance ranks were accomplished by repeated paired *t*-tests ($ns = 4$) using Bonferroni's probabilities with an experimentwise error rate of 0.05 (Snedecor and Cochran 1967). Asymmetries in dominance were tested by the binomial probability test (Snedecor and Cochran 1967).

RESULTS

The dominance relationship between the two birds of each replicate was unequivocal as the dominant won every dominance interaction both when the titmice were housed together during observations of vigilance behavior ($\bar{x} = 9.5$ interactions hr^{-1} , SD = 6.6) and when they were members of the mixed-species flocks ($\bar{x} = 3.2$ interactions hr^{-1} , SE = 1.6; one-tailed binomial *P*s < 0.032 for the probability of such an extreme outcome occurring by chance). During trials in which the subordinate was foraging in the presence of the dominant, an average of 15.8% of the supplanting attacks occurred at the feeder. Moreover, dominant titmice ($\bar{x} = 2.08$, SD = 0.35) had a significantly higher

feeding rate (kcal hr^{-1}) than did subordinates (1.62 ± 0.40) when they foraged together ($t = 4.31$, Bonferroni's $P = 0.046$, one-tailed). In contrast, the comparison between dominants ($1.80 \pm 0.40 \text{ kcal hr}^{-1}$) and subordinates ($1.37 \pm 0.46 \text{ kcal hr}^{-1}$) when they foraged solitarily was nonsignificant ($t = 1.63$, $P = 0.80$, two-tailed). Similarly, no statistical differences emerged in feeding rates while solitary compared to while feeding socially for either dominants or subordinates. Taken together, these results sustain the assumption that priority of access to a contested resource, namely the food supply at the feeder, was biased in favor of dominants.

Dominant titmice scanned at the feeder significantly longer when tested as an isolate than when allowed to feed with a subordinate titmouse present (Fig. 1). This result supports the hypothesis that vigilance is directed toward predators and, thus, is influenced by the size of the foraging group.

When the dominant and subordinate titmice were housed together in the aviary, the subordinate scanned at the feeder significantly longer than did the dominant (Fig. 1). This result supports the hypothesis that vigilance is directed toward other members of the social group and, thus, is influenced by an individual's dominance status.

Whereas dominants increased their scanning durations when solitary, the durations of scanning by subordinates in the two social contexts were statistically indistinguishable (Fig. 1). Moreover, the time spent scanning by solitary dominant and solitary subordinate titmice did not differ statistically (Fig. 1). These results further support the assertion that social dominance was the principal proximate cause of the difference in scanning durations by dominant and subordinate titmice when they were tested together.

DISCUSSION

My results support the hypotheses that vigilance is (1) directed toward predators and (2) toward higher-ranking members of a foraging group and, thus, is influenced both by the size of the foraging group and by an individual's dominance status within the group. As predicted, (1) dominant Tufted Titmice spent more time scanning upon arriving at the feeding tray when they were tested as isolates than when they were tested with a subordinate present, and (2) subordinates spent more time scanning at the feeder when a dominant conspecific was present than when tested alone.

The proximate cause of the lower feeding rate (kcal hr^{-1}) in subordinates compared to dominants when they were housed together remains open to question. This difference could reflect (1) a cost of higher conspecific-directed vigilance levels in subordinates, (2) restricted access to the feeder for subordinates, or (3) the lower energetic cost of social subordination (Hogstad 1987).

Several studies have suggested that dominant individuals of *Parus* spp. force subordinate conspecifics foraging in their company to occupy microhabitats with greater predation risk (Glase 1973; Jansson 1982; Ekman and Askenmo 1984; Ekman 1987). Ekman and Askenmo showed that when dominant Willow Tits (*Parus montanus*) were removed, subordinate first-year

birds responded by foraging higher in the canopy, where dominants usually forage. In addition, Ekman et al. (1981) documented that subordinate, first-year Willow Tits were more likely to fall victim to predators than were older, dominant birds. My results suggest another benefit of social superiority in titmice, that is, dominants may derive a greater benefit from foraging socially in terms of reduced vigilance than may lower-ranking conspecific flock-mates. Any such bias in favor of dominants in a vigilance-reduction benefit from foraging socially may allow dominants to allocate more time to foraging.

Moreover, my results prompt the speculation that in addition to any microhabitat-specific differences in vulnerability to predation, subordinates could be at greater risk of predation (or experience reduced foraging efficiency) owing to the extra constraint on their time budgets of vigilance directed toward dominant animals. Admittedly, however, vigilance for predators and vigilance for dominant group members may be complementary to some degree; subordinates sometimes at least may be able to scan the environment simultaneously for approaching predators and socially dominant animals. Alternatively, to the extent that keeping dominant flock-mates under surveillance and being vigilant for predators are synchronous tasks, dominants might improve their safety by forcing socially inferior individuals, via supplanting attacks and chases, to maintain high levels of vigilance. Such interpretations are somewhat confounded because, although it is common for free-ranging dominant and subordinate Tufted Titmice to forage within several meters of each other (pers. observ.), subordinates in this study were forced to remain within some maximum distance of dominant. Thus, the vigilance of subordinates when foraging socially might have been exaggerated.

My results differ from Hegner's (1985) results on Blue Tits (*P. caeruleus*). He found no dominance-specific differences in the partitioning of time budgets among feeding, scanning, and other activities, particularly immediately after exposure to a model Eurasian Sparrowhawk (*Accipiter nisus*). This difference in our results may be attributable to a relatively lower perceived risk of predation by the titmice in my study than by the birds in Hegner's study. It may be then that if the perceived predation risk is high, high- and low-ranking birds scan at similar rates, whereas if the danger is low, dominants may relax their scanning rate when feeding in a group.

Other studies have demonstrated that the vigilance level of foraging birds increased with decreasing group size (e.g., Powell 1974, Caraco 1979, Barnard 1980, Bertram 1980, Elgar and Catterall 1981, Studd et al. 1983, Elgar et al. 1984), with increasing distance from cover (Barnard 1980, Caraco et al. 1980a), with the appearance of a predator (Caraco et al. 1980b, Hegner 1985), with a reduction in visibility (Metcalfe 1984), when foraging in microhabitats presumed risky (Jansson 1982; Lendrem 1983; Ekman 1987), when foraging for conspicuous rather than cryptic prey (Lawrence 1985), and when an alarm call was given (Sullivan 1984b). These studies share the assumption that the detection of predators is the primary function of vig-

ilance. Indeed, Knight and Knight (1986) have provided the only evidence that vigilance in birds that feed in social groups has the additional function of detecting kleptoparasitic attacks launched by conspecific flock-mates. They found a positive correlation between vigilance and group size for groups of eight to 14 Bald Eagles (*Haliaeetus leucocephalus*). The results of the present study constitute the first experimental demonstration that vigilance levels in birds can be influenced by an individual's dominance status (but cf. Waite 1986). Unfortunately, however, because the birds in this study were not aged and the sex was only inferred, I cannot eliminate the possibility that the vigilance differences observed were partly attributable to differences in age and sex per se that were correlates of dominance status.

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